

MACROALGAL NUTRIENT DYNAMICS IN UPPER NEWPORT BAY

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July 3, 2002

INTRODUCTION

Newport Bay is the second largest estuarine embayment in southern California and provides critical natural habitat for terrestrial and aquatic species. The upper portion of the Bay is a state ecological reserve and serves as refuge, foraging areas, and breeding grounds for a number of threatened and endangered species. The Bay also provides significant spawning and nursery habitats for commercially and recreationally fished species. However, the Bay is subject to anthropogenic stressors. For example, high nutrient loads from the surrounding watershed have resulted in excessive growth of macroalgae (*Enteromorpha* and *Ulva* spp.) and impairment of the Bay's beneficial uses.

Macroalgae exhibit distinct seasonal patterns of biomass accumulation in Upper Newport Bay (UNB). *Enteromorpha* and *Ulva* spp. are generally sparse in the winter and early spring (December-April) when growth is likely limited by environmental factors such as light, temperature, and flow. *Enteromorpha* and *Ulva* are prolific throughout the summer and early fall months (June-October) when light and temperature conditions are optimal for maximum growth. During these months, macroalgal biomass may be limited by factors such as nutrients, space, or herbivory. While the seasonal patterns of algal blooms in UNB and the biomass of algae during these events is documented to some degree, the relative importance of the different factors that may control macroalgal biomass are not yet fully understood.

In part due to the excessive growth of macroalgae, UNB has been added to the Clean Water Act 303(d) list for nutrients, as well as other constituents. The 303(d) listing precipitated the development and adoption of a Total Maximum Daily Load (TMDL) for nitrogen (N) and phosphorus (P) in San Diego Creek, the largest tributary to UNB, in 1998. The implementation phase of the nutrient TMDL has several elements, one of which calls for the evaluation of N and P water quality objectives (WQOs).

A report titled *Comparison of Nutrient Inputs, Water Column Concentrations, and Macroalgal Biomass in Upper Newport Bay, California* (Schiff and Kamer, 2000) was the first step toward evaluating the current total inorganic nitrogen (TIN) WQOs. The goal of the report was to find published studies of estuaries in which water quality and macroalgal biomass data had been collected synoptically and to determine if the WQOs in San Diego Creek were overly conservative, not conservative enough, or if insufficient data existed to evaluate the appropriateness of the current WQOs for N and P. The report concluded that insufficient data were available to make this assessment based upon several factors. First, there was a limited amount of synoptic water quality and quantitative macroalgal abundance data from other estuaries. Second, there was no relationship between water quality and macroalgae; it was not possible to reliably predict macroalgal biomass from water column nutrient concentrations. Third, southern California estuaries were distinctly different from other estuaries in the US and abroad, which limits attempts to extrapolate data from other regions and apply them locally. Fourth, significant secondary mechanisms involved in nutrient dynamics were not fully understood and needed to be investigated in order to understand the impacts of nutrient loads on estuaries.

Since there was no relationship between water column N or P and macroalgal biomass, there was a clear need for mechanistic studies investigating the processes in Upper Newport Bay (UNB)

that control macroalgal biomass. Increased understanding of the processes and mechanisms that regulate the growth and biomass accumulation of *Enteromorpha* and *Ulva* spp. is paramount to making informed management decisions for estuaries such as UNB. Studies identified as high priority by Schiff and Kamer (2000) were to: 1) investigate the contribution of nutrients from estuarine sediments to macroalgal growth and tissue nutrient content; 2) determine if N or P is the nutrient most limiting to macroalgae; 3) measure rates of N and P uptake by *Enteromorpha intestinalis* and *Ulva expansa*, the dominant, green, bloom-forming macroalgal species; and 4) investigate the effects of variation in the frequency and concentration of nutrient pulses on macroalgal growth and tissue nutrient content. These are some of the important mechanisms that may enable macroalgae to bloom under enriched conditions of southern California estuaries.

PROCESS-BASED STUDIES

Effects of estuarine sediments on macroalgae

Biomass of *Enteromorpha* and *Ulva* spp. is regulated, in large part, by availability of dissolved nutrients. These algae can obtain the dissolved nutrients they need from multiple sources, such as the water column or estuarine sediments (i.e. dissolved nutrient flux from porewaters). In estuaries, water column nutrient levels are generally higher near the head of the system, where rivers flow in, and decrease toward the mouth or the opening to the ocean. Therefore, the availability of water column N to macroalgae usually decreases along a spatial gradient within an estuary from the head toward the mouth. Nutrient concentrations of estuarine sediments may vary spatially as well within an estuary. This variation is likely controlled by sediment quality (i.e., grain size, organic content), which may not vary linearly along a spatial gradient. As a result, estuarine sediments may also be a significant source of nutrients to macroalgae, particularly when water column nutrients are low. However, there is little empirical data on the extent to which dissolved nutrients fluxing from estuarine sediments are either taken up by macroalgae or are of benefit to macroalgae. Our objective was to determine the importance of water column vs. sediments as sources of nutrients to macroalgae in UNB.

We hypothesized that the importance of water column vs. sediment sources of nutrients to *Enteromorpha intestinalis* varied along a nutrient resource gradient within UNB. We tested this hypothesis by constructing experimental units using water and sediments collected from 3 sites in UNB. We measured changes in water column and sediment nutrients in three sets of experimental units for each site: sediments + water; sediments + water + *E. intestinalis* (algae); inert sand (no nutrients) + water + algae. In units containing algae, we measured growth and tissue nutrients (N and P).

The importance of the water column versus sediments as sources of nutrients to *Enteromorpha intestinalis* varied with the magnitude of the different sources. When initial water column dissolved inorganic N (DIN) and PO₄ levels were low, nutrients from estuarine sediments increased *E. intestinalis* growth and tissue nutrient concentrations. Macroalgal growth and tissue P increased with increases in initial sediment nutrient concentrations. In units from the site where initial water column DIN was high, there was no effect of estuarine sediments on algal growth or tissue N content. However, reduced salinity of water from this site may have limited macroalgal growth overall, thereby masking any effects of sediment nutrients. Water column

inorganic N was consistently depleted throughout the experiment, regardless of initial water column N concentration. Thus, the water column was a primary source of nutrients to the algae when water column nutrient supply was high, and the sediments supplemented nutrient supply to the algae when water column nutrient sources were low. The sediments acted as both a source and a sink of nutrients in this experiment, depending on water column nutrient concentrations.

These data provide direct experimental evidence of the role of sediment nutrients in estuarine nutrient dynamics. Macroalgae can utilize nutrients stored in estuarine sediments, which implies that nutrient inputs and the response of increased biomass of macroalgae may be temporally uncoupled via storage in the sediments. Therefore, calculations of nutrient loads to estuaries or annual budgets for these systems should include fluxes from the sediments as well as loading from the watershed.

Nitrogen vs. phosphorus limitation of macroalgae

The growth of macroalgae is controlled, in large part, by nutrients as well as salinity, light, and temperature. N and P are the two most common nutrients that limit macroalgal growth. However, nutrient limitation of macroalgae in an estuary may vary along a gradient of resource availability due to differential rates of nutrient processing (e.g., P mineralizes much more quickly than N). Therefore, we investigated N and P limitation of macroalgae along a spatial nutrient gradient in UNB.

Enteromorpha intestinalis and water were collected from 5 sites ranging from the lower end of UNB to the head near San Diego Creek. Portions of the water from each site were amended with nutrients to create 4 experimental solutions (control [C], nitrogen enrichment [+N], phosphorus enrichment [+P], and nitrogen and phosphorus enrichment [+N+P]). Algae were added to replicate experimental units, each filled with one of the experimental solutions. We measured water column nutrient concentrations in each experimental unit for three weeks and, at the end of the experiment, we measured *E. intestinalis* biomass and tissue N and P concentrations.

Biomass of *Enteromorpha intestinalis* from 3 of 5 sites increased with N enrichment alone and increased further when P was added in combination with N. This indicated that N was the most limiting nutrient and that P was the next most limiting nutrient after N. Growth increased among algae from the most seaward site toward the head of the estuary reflecting initial tissue nutrient concentrations and ambient water column N supplies. In contrast, growth of *E. intestinalis* from the site closest to the head of the estuary after additions of N and P was moderate relative to the other sites and, therefore, may have been limited by a factor other than nutrients. Final tissue N and P concentrations reflected both initial water column levels and N and P enrichment, respectively. Depletion of tissue nutrients during the experiment suggested that algae were growing on internal reserves of nutrients.

Since N was the nutrient most limiting to *Enteromorpha intestinalis*, a reduction of the supply of N to UNB should result in a decrease in macroalgal biomass within the system. Since P was also limiting to macroalgae at several sites, reductions in P supply in conjunction with reductions in N supply may also decrease macroalgae in UNB.

Uptake of nitrogen and phosphorus by *Enteromorpha intestinalis* and *Ulva expansa*

As both N and P may limit macroalgal biomass in UNB, the uptake dynamics of both nutrients may be important in the system's nutrient and macroalgal bloom dynamics. Macroalgal nutrient uptake rates vary with a suite of factors including, but not limited to, initial algal tissue nutrient status. Generally, N uptake rates increase as tissue N concentration decreases, reflecting N starvation and increased N demand. Nutrient uptake rates also vary with external substrate concentration. The objective of this study was to measure the rates of inorganic N and P uptake by *Enteromorpha intestinalis* and *Ulva expansa* under varying initial water column concentrations and algal tissue nutrient concentrations representative of levels measured in UNB.

Rates of N and P uptake by *Enteromorpha intestinalis* and *Ulva expansa* were investigated in 4 separate experiments. We varied initial water column nutrient concentrations (low, medium and high) and initial algal tissue nutrient status (enriched vs. depleted). In each experiment, uptake of either N or P by either *E. intestinalis* or *U. expansa* was measured at 1, 2, 4, 8, 12, and 24 h. Uptake rates of inorganic nitrogen and phosphorus were determined by measuring the disappearance of inorganic nutrients from solution over time.

Enteromorpha intestinalis and *Ulva expansa* exhibited a high affinity for N across all treatments, but little or no affinity for P. In the low water column concentration treatments, *E. intestinalis* and *U. expansa* removed all measurable NO_3 from the water within 8 and 12 h, respectively. Nutrient depleted algae consistently removed more NO_3 than enriched algae over each sampling interval. Maximum rates of NO_3 uptake exceeded $200 \mu\text{moles g dry wt}^{-1} \text{ h}^{-1}$ by *E. intestinalis* and $125 \mu\text{moles g dry wt}^{-1} \text{ h}^{-1}$ by *U. expansa*. These rates were up to two orders of magnitude greater than rates measured for other species, but similar to rates measured for these species by other researchers.

Maximum rates of NO_3 uptake increased with increasing initial water column nutrient concentrations, indicating a relationship between uptake and external substrate concentration. Nutrient uptake rates were highly variable over 24 h, indicating surge, internally controlled, and externally controlled phases of nutrient uptake. Over the first 2 h of the *Enteromorpha intestinalis* NO_3 uptake experiment, uptake rates went from the maximum measured to negative rates, indicating a release of N from algal tissue. Similarly, *U. expansa* NO_3 uptake rates were greatest in the first hour, decreased to zero in the second hour, and then resumed. For both species, depleted algae showed greater increases in tissue N and P concentration in response to water column nutrient supplies than enriched algae did, and the tissue N increases were concentration dependent.

Initial tissue nutrient status was very important in determining the rate of N uptake by both *Ulva expansa* and *Enteromorpha intestinalis*. Algae depleted of N before the experiments had greater demands for N and therefore higher uptake rates than enriched algae. Other critical factors in nutrient uptake by macroalgae were nutrient concentration in the water column and the various phases of nutrient uptake. Therefore, prediction of nutrient uptake rates cannot be based on nutrient supply or concentration alone. In order to accurately predict uptake of nutrients by macroalgae in the field, it is also necessary to know the nutrient history of the algae and to measure uptake rates over time scales that

encompass the different phases of nutrient uptake. The high N uptake rates exhibited by *E. intestinalis* and *U. expansa* are characteristics that explain their success in UNB, where N availability can be spatially and temporally patchy, and demonstrate the difficulty in controlling blooms.

Effects of frequency and concentration of nutrient pulses on macroalgae

The ways in which temporal variation in the supply of nutrients to macroalgae may affect growth and tissue nutrient status are largely unknown. Nutrient inputs to estuaries can vary over temporal scales from hours to months, and macroalgae can store nutrients and use reserves for growth when external nutrient supplies are low. This strategy likely enables them to succeed in environments such as estuaries with episodic inputs of nutrients. Our objective was to quantify how the frequency and concentration of nutrients supplied to *Enteromorpha intestinalis* and *Ulva expansa* affect growth and tissue nutrient dynamics.

Over a 28-day period, *Enteromorpha intestinalis* and *Ulva expansa* were each given equal supplies of NO₃-N (28 mg) and PO₄-P (6.2 mg) via pulses of different frequency and therefore different concentration. NO₃-N doses given to 10 g wet wt of algae in 1 L seawater were: 1 mg (once per day), 7 mg (once per week), 14 mg (once per two weeks), or 28 mg (once per month). Phosphorus was also added in a 10:1 (molar) ratio. Water column nutrient levels were monitored throughout the course of the experiment. Algal biomass and tissue N and P concentrations were measured at the end of the experiment.

Enteromorpha intestinalis and *Ulva expansa* responded to all nutrient doses used in this study. Growth in both algae increased most with daily doses, although significant growth of both algae was measured for all frequencies of doses. Therefore, algae were able to store enough nutrients from the large, one-time pulses to sustain positive increases in biomass in low nutrient environments for up to 28 d. Tissue nutrient content was also related to the frequency and concentration of the doses. Total mass of N and P in algal tissue (mg unit⁻¹) increased as frequency of doses increased. Overall, tissue N concentrations were greater in *U. expansa*, and tissue P concentrations were greater in *E. intestinalis*. *E. intestinalis* and *U. expansa* removed substantial portions of the nutrient doses. Twenty-nine % to 96% of added nutrients were removed from the water by algae within 24 h.

Storage of pulsed nutrients in macroalgal tissues means that the effects of nutrient pulses on macroalgae may last longer than the nutrient pulse itself remains in the water column. Due to nutrient storage in algal tissue, effects of large nutrient pulses may be as important and persistent in natural systems as chronic, low-grade nutrient inputs. This effect may be exacerbated in natural systems due to sediment storage and release of nutrients. The frequency of nutrient inputs to coastal systems may be critical in determining macroalgal biomass, and temporal scales should be taken into account when regulating nutrient loads in order to minimize macroalgal biomass.

CONCLUSIONS

- *Sediments were an important source of nutrients to macroalgae when water column supply was low, and contributions from sediments need to be incorporated into nutrient budgets for UNB.*

Growth and tissue nutrient concentrations (N and P) of *Enteromorpha intestinalis* were greater in the presence of estuarine sediments containing measurable nutrients compared to nutrient-free sediment controls. Moreover, macroalgal growth and tissue concentrations increased with increases in initial sediment nutrient concentrations. Similarly, Lavery and McComb (1981) documented macroalgal growth after exposure to estuarine sediments. Since sediments represent a potentially significant source of nutrients to macroalgae, further studies to quantify the flux of N and P from sediments will be required for a basic understanding of nutrient cycling and utilization in UNB.

- *N was the most limiting nutrient to macroalgal growth. P was secondarily limiting at some sites within UNB.*

When N and P were added to experimental units with *Enteromorpha intestinalis* from UNB, biomass of algae from 3 sites increased with N only additions. Biomass increased further when P was added in combination with N, but no increases in biomass were seen with P only additions. Therefore, strategies to reduce macroalgal biomass in UNB should focus primarily on reductions in N loads to the Bay and secondarily on P loads.

- *Nitrogen uptake rates were a function of water column nutrient concentration and the recent exposure of algae to nutrients.*

Enteromorpha intestinalis and *Ulva expansa* are very efficient algae at consuming NO_3 with uptake rates measured up to $>200 \mu\text{moles g dry wt}^{-1} \text{ h}^{-1}$. These rates are up to an order of magnitude higher than other macroalgae such as *Codium* or *Gracilaria*. Uptake rates increased with water column concentrations; higher initial water column NO_3 concentrations resulted in higher rates of NO_3 uptake. In addition, nutrient depleted algae had consistently higher rates of nutrient uptake than algae that were enriched with NO_3 . Short-term temporal fluctuations in uptake were a function of algal physiology (i.e., surge uptake, internally controlled uptake, and externally controlled uptake). Each of these factors is important for accurately predicting nutrient uptake and macroalgal growth.

- *Algae efficiently stored large pulses of nutrients and used them for growth when nutrient supply was low.*

Enteromorpha intestinalis and *Ulva expansa* grew most and had the greatest increases in tissue N and P content with daily, low concentration nutrient additions (cumulative dose of 28 mg N and 6 mg P over 28 days). As demonstrated earlier, however, these algae are also efficient scavengers of nutrients. As a result, significant algal growth was observed in all treatments, regardless of frequency of nutrient addition, including a single dose of

28 mg N and 6 mg P. Therefore, large infrequent nutrient loads should be considered in any macroalgae control plan, in addition to controlling chronic, low-grade nutrient inputs.

RECOMMENDATIONS

There are several steps that can be taken to further understand the relationship between nutrients and macroalgae so that regulators and stakeholders can set water quality limits and reduce macroalgal biomass, and its effects, in UNB. These activities can continue in parallel with other management actions targeted at reducing or controlling macroalgal biomass.

- *Improved estimates of nutrient loading from sediments are needed if accurate nutrient budgets for UNB are desired.*

A nutrient budget for UNB will not be accurate unless it incorporates nutrient loading from sediments. Research in other estuarine systems has shown that the magnitude and direction of sediment N and P flux vary temporally and spatially. Therefore, in order to achieve a comprehensive understanding of nutrient loading to the Bay, sediment-water column nutrient exchange should be quantified at several sites in UNB over an annual cycle. In addition, sediment-water column nutrient dynamics can vary with changing physical conditions (salinity, oxygen levels, sediment grain size). Therefore, sediment-water column nutrient flux should be estimated under varying environmental conditions.

- *The mechanism and process studies conducted herein are extremely useful for creating a dynamic nutrient model that predicts algal growth in UNB.*

Building a believable nutrient-macroalgal model is a complex, but worthwhile undertaking. The process for creating such a model requires many steps building from a basic nutrient budget, quantifying parameters that characterize the multitude of processes that occur in the Bay, to calibrating and validating the model with locally collected empirical data. The benefit of a well-calibrated and validated model is the ability to predict macroalgal biomass based on knowledge of nutrient inputs to UNB.

Resource Management Associates, Inc. (RMA) has developed a water quality model for UNB in support of the nutrient TMDL. The RMA modeling effort has completed some of the initial steps in the model building process. RMA relied on values and rate constants from studies conducted in other geographic regions for determining the macroalgal responses to nutrients in UNB. The literature review conducted by Schiff and Kamer (2000), however, showed that UNB is dissimilar from other geographic regions. Based on the studies described herein, we now have local site-specific data on rates and processes in UNB, which will lead to more accurate model-based predictions of water quality and macroalgae in UNB.

Now that site-specific data is available for UNB, we recommend that one of the first steps is to update and re-evaluate the RMA model to determine its ability to model this system. Additional validation data will be necessary for this re-evaluation. We recommend that additional data collection be integrated with the existing UNB Regional Monitoring Program to enhance cost-efficiency.

- *Once sufficiently validated, the dynamic model should be used to assess the most effective and efficient strategies for achieving management endpoints.*

The power of a dynamic nutrient model is its predictive ability. The model then becomes an extremely useful management tool that regulators and stakeholders can use to run multiple implementation scenarios for reducing macroalgal biomass. In this way, UNB managers can evaluate the most effective and efficient mechanisms for achieving management endpoints of concern, including setting realistic concentration- or load-based water quality objectives.

REFERENCES

Schiff, K. and K. Kamer. 2000. Comparison of nutrient inputs, water column concentrations, and macroalgal biomass in Upper Newport Bay, California. Southern California Coastal Water Research Project, Westminster, CA.